thus ascribed to terrestrial and not to solar influence.

THE NEED OF A METEOROLOGICAL LABORATORY

PROFESSOR CLEVELAND ABBE, who in January last was awarded the Symons Gold Medal by the Royal Meteorological Society for his contributions "to instrumental, statistical, dynamical and thermodynamical meteorology and forecasting," has communicated an interesting paper to the Franklin Institute, Philadelphia, on "The Obstacles to the Progress of Meteorology." In it he says that even if we had perfect observations and records for ages past, with free air data up to heights of ten or fifteen miles, together with daily weather maps for the whole northern hemisphere, perfect weather predictions could not now be made because of "our ignorance of many details as to the laws that govern the atmosphere and our inability to put even what little knowledge we have into such a form that it can be perfectly utilized by the forecaster." He shows that in every branch of science progress has been accomplished mainly through laboratory observation and experiment, guided by the spirit of mathematics. He therefore says in concluding:

What I most long to see, and what I believe is of fundamental importance in atmospherics—the want of which is a real obstacle—is the existence of a laboratory building specifically adapted to atmospheric experiments, and the association therewith of able students trained in mathematics, physics and mechanics. When all this is realized the intellectual work that will there be done will gradually remove all obstacles to the eventual perfection of our knowledge of the atmosphere.

NEW BOOKS

AMONG the books which have recently appeared are: (1) "Climate and Weather," by H. N. Dickson. London, Williams and Norgate, 8vo, 256 pp., 1s. net. (2) "Instructions Météorologiques," by Alfred Angot. 5th edition. Paris, Gauthier-Villars, 8vo, 161 pp. (3) "International Catalogue of Scientific Literature"—"Meteorology, including Terrestrial Magnetism." London, Harrison and Sons, 8vo, 238 pp., 15s. (4) "Atlas Photographique des Nauges," by J. Loisel. 8 pp. + 10 pl., Paris, G. Thomas, 18 fr. (5) "The Structure of the Atmosphere in Clear Weather: a Study of Soundings with Pilot Balloons," by C. J. P. Cave. 4vo, 144 pp., Cambridge University Press, 10s. 6d. net. (6) "Meteorological Instruments and Weather Forecasts," by H. T. Davidge. London, P. Marshall and Co., 6d. net. (7) "Barometers and the Measurement of Atmospheric Pressure," by C. F. Marvin. 4th edition, 8vo, 110 pp., Washington, U. S. Weather Bureau, Instrument Division, Circular F. (8) "Evaporation from Irrigated Soils," by S. Fortier and S. H. Beckett, 8vo, 77 pp.. Washington, U. S. Office of Experiment Stations, Bulletin 248.

ANDREW H. PALMER

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SPECIAL ARTICLES

THE PHYSIOLOGICAL SIGNIFICANCE OF THE SEGMENTED STRUCTURE OF THE STRIATED MUSCLE FIBER

THE question of the physiological significance of the segmented structure of striated muscle fibers remains for most physiologists one of the standing enigmas of their science. What relation—if any—has this structure to the power of rapid and instantly reversible contraction which is the distinctive peculiarity of this tissue? No entirely satisfactory answer to this question has hitherto been found; those which have been proposed are as diverse as their authors' conceptions of the ultimate of the difficulty lies here. The histological literature is full of contradictions and hence —since all can not be right—of misinterpretations. Before agreement can be reached on the physiological question, it is evident that a clear and satisfactory conception of the essential structure of the living muscle-cell is necessary. Many of the structural minutiæ visible in histological preparations vary according to the nature of the treatment accorded the tissue. Their physiological significance is thus doubtful. During recent years

a certain change in the procedure of investigators has become apparent. Experience of the readiness with which the structure or " aggregation-state " of a colloidal system may be altered has made it clear that such structures are not always to be regarded as preexistent in the living tissue. They are rather to be regarded as appearances from which, on the basis of an adequate knowledge of the behavior of colloidal systems under similar treatment, inferences may be drawn as to the original disposition and state of the colloidal material in the living system. Inferences so drawn require to be controlled by an exact knowledge of the structural appearances in living muscle during both rest and contraction. Hence recent investigators—as Hürthle and Meigs—have relied mainly on direct and photographic observation of living muscle fibers. But even results so gained show considerable disagreement in detail, and unfortunately they have proved compatible with diametrically opposed conceptions of the essential nature of the contractile process.

Certain definite conclusions have, however, been reached. It is agreed that the contractile elements are solid fibrils—consisting supposedly of water-swollen myosin—which are embedded in a more fluid sarcoplasm; the fibrils are not optically homogeneous, but exhibit a regular alternation of longer segments consisting of more refractive and largely doubly refractive (anisotropic) material, with shorter less refractive segments showing little or no double refraction (isotropic). In the voluntary muscle-cell of vertebrates the fibrils are crowded together closely, and in such a manner that the adjacent anisotropic and isotropic segments of different fibrils lie at the same level; this level is perpendicular to the long axis of the muscle cell, hence the latter, as a whole, shows the characteristic cross-striation. It is this peculiarity of parallelism in the disposition of the fibrillar segments which Hürthle characterizes as " schwer verständlich." It plainly suggests that the fibrils are laterally conjoined in a definite manner so as to form a system coherent throughout the cell. Conceptions differ, however, as to the

ultimate structure of the individual fibrils, and particularly as to the nature of the conditions producing the segmented appearance.

I shall not attempt in this place to discriminate minutely between conflicting views regarding structure; my aim is merely to show that a segmented structure is in itself—and largely irrespective of the precise nature of the structural conditions that determine the segmentation—a condition favorable to rapid and quickly reversible changes of form. The questions to be discussed are thus: What mechanical advantage does a rapidly contractile colloidal system like muscle derive (1) from having its fibrils regularly and minutely segmented, and (2) from having the corresponding segments of adjacent fibrils at the same level?

Considered from a physico-chemical point of view, the individual muscle-fibril forms a colloidal system in which regions showing a well-marked contrast in optical and apparently also in chemical properties (evidence from staining) alternate regularly with one another. It is, however, doubtful if the alternate segments differ in their essential chemical constitution; the evidence seems rather to indicate that the same colloidal material forms the solid substratum of the fibril throughout its entire length, but that this material differs in its state of aggregation in alternate segments. The colloidal particles must be regarded as forming a coherent system throughout the entire fibril, as in a gel; otherwise the fibril would have no tensile strength. Between the coherent particles of any gel are interstitial fluid-containing spaces.[1] If the fibril is essentially a gel, as thus assumed, with myosin as the chief colloid, its physical

[1] The recent observations of Bachmann, made in Zsigmondy's laboratory, on the ultramicroscopic structure of gels, show that during gelation the motion of the submicrons changes from one of a free translatory character to one in which the submicrons undergo only slight vibratory movements about fixed positions of equilibrium. There is thus in gelation an aggregation of submicrons and amicrons to form a coherent system, with fluid-containing interspaces. Cf. *Zeitschrift für anorganische Chemie*, 1911, p. 125.

condition from segment to segment can vary only in the concentration and state of aggregation of its colloid material. There are indications that the colloidal particles (probably submicrons) are more densely aggregated in the dim bands and less densely in the light; in this case the interstitial spaces must be smaller in the dim and larger in the light bands; *i. e.*, the proportion of displaceable fluid material is greater in the light bands, the latter, so to speak, having the looser texture of the two. Such a conception explains many characteristic observations, such as the beaded form shown by fibrils under certain conditions; the greater compressibility of the isotropic segments (indicating a greater fluidity), as shown by the experiments of Haycraft, who obtained impressions of the segmented structure by pressing living fibers against collodion; the facts that the double refraction appears rather to diminish than entirely to disappear in the light bands, and that adsorbed coloring materials, such as hæmatoxylin, though taken up by the whole fibril, are extracted most readily from the isotropic segments, just as though the adsorbing surface were there relatively less. Hürthle also compares the material composing the fibril to a gel; he regards this as chemically homogeneous throughout, but as differing in its physical condition in alternate segments. He adduces the analogy of the nodes in a stretched vibrating string, implying that the differences between the alternating segments are purely physical and independent of differences in chemical composition. Although it is doubtful that marked differences in the colloidal aggregation-state could exist between adjacent segments without at least some quantitative differences of chemical composition due to differences of adsorption, etc., yet the essential conception of the fibril as essentially homogeneous in its chemical composition is not altered by recognizing the existence of a segmented structure of the above conceived kind.

On this view the fibril is to be regarded as a column of colloidal material having the essential properties of a gel—*i. e.*, a system in which the colloidal particles cohere; the particles, however, are not homogeneously distributed in this gel, but are relatively densely aggregated in the anisotropic segments and loosely in the isotropic; in the latter the interstitial fluid-containing spaces are therefore relatively larger. It should be noted that in all muscles the isotropic segments are shorter than the anisotropic; also that the best photographic evidence indicates that the actual shortening is confined to the anisotropic regions of the fibril, *i. e.*, to the regions where the colloidal particles are the most closely aggregated. The significance of this will be apparent later.

The considerations urged in the preceding paragraph relate to the individual fibril and do not explain the lateral coherence of the fibrils. It seems clear, from the fact that the striation is preserved during contraction, that transverse connections must exist between adjacent fibrils, otherwise the latter would certainly undergo relative displacement more frequently than observation shows to be the case. But the histological evidence of such cross connections is imperfect, although the view seems well founded that the appearances known as Hensen's and Krause's lines (*M* and *Z* lines) correspond to regions where adjacent fibrils are laterally conjoined. This view is supported by Heidenhain on the basis of numerous observations on fixed muscle of various kinds; and a continuity of the *Z*-lines from fibril to fibril, even when the latter are separated by some distance, is clearly apparent in some of Meigs's photographs. Both of these appearances, especially the *Z* or intermediate line, have been interpreted as membranes subdividing the fibrils at segmental intervals; but they seem to lack the continuity which such a conception demands. A continuous membrane would show definite optical appearances due to reflection of light at its surface. The so-called *J*-lines, which suggest such reflection and hence support this conception, are variable and often unapparent. On the other hand, the existence of narrow cross-connections between adjacent fibrils would undoubtedly account for the observed

appearances. I am, therefore, inclined to favor this interpretation. According to this conception these structures are of no essential importance in contraction except in so far as they prevent relative displacement of adjacent fibrils. But such displacement, if permitted, would interfere with the contractile properties of the system, as I shall show later, so that the physiological rôle thus assigned to these structures may after all be indispensable. This view is however quite opposed to any hypothesis—like that of Pütter —which regards the intermediate lines as corresponding to membranes whose state of permeability determines the degree of osmotic distension of the muscle segments, and so the state of contraction. The evidence of their membrane character seems insufficient to serve as support for such a speculative view as this. On the other hand, the lateral coherence of the fibrils is an undoubted fact which must have a structural basis, and direct observations exist which indicate that at least the Z lines—which appear to be the more constant of the two—do in fact cross the intervals between the fibrils. Structures thus continuous from fibril to fibril are most naturally interpreted as connectives.

We may now consider the physiological problem as to the nature of the essential physical changes which form the direct condition of the characteristic mechanical deformation of active muscle. The precise nature of the energy-yielding metabolic process need not concern us here. As well known, various more or less seriously conflicting hypotheses exist. There is considerable evidence of a displacement of fluid within the contractile elements during activity, and this fact has led to the development of theories which assign to this transfer of fluid the essential rôle in the process of contraction. Thus Engelmann and many others have referred the process to a water-absorption or swelling of certain structural elements—just as gelatine sheets swell in water, and more rapidly when the water is warm or acidulated than when it is cold or neutral. The general structural conception put forward some time ago by McDougall,

and recently favored by Meigs and others, has been that of a tissue composed of elements comparable to somewhat elongated or spindle-shaped fluid-containing sacs with inextensible walls; these elements on distension approach a spherical form, with consequent approximation of their opposite ends. A certain degree of shortening (about 37 per cent.) may thus theoretically be accounted for. That the actual shortening often greatly exceeds this proportion is unfavorable to such hypotheses, though perhaps not necessarily incompatible with them. The structural conditions might conceivably be such that the swelling elements at their maximal normal distension adopt a form in which the ratio of transverse to longitudinal diameters—assuming these to correspond with those of the muscle-cell—is increased sufficiently to account for a much greater degree of shortening than the above. All that would be necessary to render such a hypothesis adequate in this respect would be to assign a certain definite structure and form to the elements. Take for instance the case of a tissue composed of structural units resembling the extended elaters of the spores of *Equisetum;* as is well known, these structures when slightly moistened wind themselves closely around the spore; the total diameter of the system, spore *plus* elaters, may thus be reduced to a small fraction of the original diameter as measured between the tips of the extended elaters. One might conceive of muscle as composed of elements similar in contractile properties to elaters, united in a definite manner to form a contractile system; and it would no doubt be possible, by exercising some ingenuity, to reconcile such a conception with the main histological appearances. Hypotheses that refer the contraction to swelling of the contractile elements are thus not to be dismissed by advocates of other views as inadmissible on the ground of purely geometrical considerations. The objections to this type of explanation are of quite another nature; and since they are in my opinion sufficiently weighty to render it extremely doubtful that this kind of physical charge could ever form the basis

of a movement so rapid, responsive and quickly reversible as muscular contraction, I shall briefly recapitulate what I consider to be the chief inadequacies of such hypotheses.

(1) The time required for a contraction and relaxation due to swelling-changes in the colloidal contractile elements—involving both the incorporation of water into the colloid and its release—seems to be too great. Pauli, indeed, once estimated that if the elements have the swelling properties of gelatine discs, and the same surface-volume ratio as the muscle-segments, the rate of swelling might be sufficient to account for a contraction as rapid as that of frogs' muscle. But the single twitch may be many times shorter than this, as in insects' wing-muscle, where moreover the muscle-segments are larger than in vertebrate muscle. It is of course possible to reply to this objection that the actual elements concerned may be much smaller than the visible muscle-segments. Still, in any case, since the single-twitch curve of striated muscle is symmetrical, the rate of the water-absorption would have to correspond in its time-relations with that of the water-loss. These curves, however, have been shown to follow different courses in those cases which have been actually investigated (by van Bemmelen). (2) A more serious difficulty is that the temperature-coefficient of the mechanical energy of contraction, according to Bernstein's investigations, is *negative; i. e.,* within a normal range—up to 30°—the lifting power of the twitch is *increased,* with a given intensity of stimulus, by lowering the temperature. The temperature-coefficient of swelling processes is however positive and large, like that of chemical reactions; that of surface tension, on the contrary, is negative. Bernstein's experiments must be regarded as very significant, since the temperature-coefficients of the chemical changes concerned in contraction are of course positive; the above result would seem therefore quite unaccountable if a chemical change, like the production of acid, preceded and formed the condition of the contractile change. These experiments thus appear to indicate, first, that the process immediately

conditioning the contraction is only indirectly dependent on a chemical change,[2] and, second, since this process has a negative temperature-coefficient (a distinctive peculiarity of surface-tension), that a change of surface-tension in the ultimate contractile elements is the direct source of the energy of contraction. (3) A further disadvantage of the " swelling-hypotheses "—as contrasted with the surface-tension hypothesis—is that they offer no suggestion as to the nature of the connection between the electrical variation accompanying contraction and the actual contractile process. In electrical stimulation a change in the electrical polarization of the plasma-membrane is almost certainly the essential or critical event. If the membrane enclosing a colloidal system, such as a muscle-cell, changes its polarization, a corresponding change of polarization must occur at *all* of the electrically polarized surfaces within the system thus enclosed,[3] including presumably the surfaces of the colloidal particles composing the contractile elements. Changes of electrical polarization at surfaces are definitely known to alter the surface-tension. On the other hand, the relation assumed to exist between the polarization-change of stimulation and the swelling of the colloidal elements, according to the hypothesis under consideration, must be exceedingly indirect. A chemical change must first be assumed to occur, producing substances, supposedly acid, which increase the swelling properties of the colloid. There is nothing unreasonable in this view, but it fails to suggest any explanation of the close parallelism which exists between the electrical and the contractile processes in active muscle. The interdependence between the two is undoubtedly intimate, and is readily intelligible on the hypothesis just outlined

[2] Resembling in this respect the plant-movements due to changes in the permeability of the plasma-membranes of turgid cells (in *Mimosa, Dionæa,* etc.).

[3] Since the electrical potential of the whole cell-interior changes, and with it one of the factors in the conditions of equilibrium of the electrical double layers at the polarized surfaces within the cell.

that alterations of the surface-tension of the contractile elements, conditioned by variations in their electrical surface-polarization, form the immediate condition of contraction. Any hypothesis which fails to explain this interconnection must be regarded as seriously deficient.

I shall now discuss more fully what is usually regarded as the alternative hypothesis, namely, that the contractile energy is due to changes in the surface-tension of certain muscle-elements. In contraction the surface-tension of these elements is supposedly increased. If this increase of tension is sufficiently great, and the area of the active surface sufficiently large, the transformable surface-energy, which is measured by the product of these two factors, may be sufficient to account for the work done by muscle in contraction. The main question is whether the evidence justifies us in assuming the existence of such conditions in the living muscle-cell. Now the possible range of alteration in the surface-tension of the colloidal contractile elements under the influence of changing electrical polarization is undoubtedly small—almost certainly less than ten dynes per linear centimeter—so that in order to develop the force observed in contraction a very large active surface would be required. Bernstein has shown that any possible alteration of surface-tension at the surface of the muscle-fibrils is quite insufficient to account for the work done by contracting muscle; and he has therefore assumed that in its ultimate structure the fibril is built up out of smaller ellipsoid contractile elements, by the alteration of whose surface-tension the contraction of the whole fibril is produced. By ascribing sufficiently small dimensions to these elements it is possible hypothetically to enlarge the surface to the required degree. But is such an assumption reconcilable with our present knowledge of muscle structure? In Hürthle's photographs the fibril-segments show a subdivision into narrower rodlet-like structures ("Stäbchen") which he regards as the ultimate contractile elements. The united surface-area even of these elements is also far from

sufficient to meet the requirements. There are thus no microscopically demonstrable structures corresponding to Bernstein's hypothetical ellipsoids. It is necessary, if the hypothesis is not to be abandoned, to inquire if still smaller elements may not exist by the alteration of whose surface-tension the requisite mechanical energy may be produced. There is, as I have pointed out elsewhere, good reason to regard the ultimate colloidal particles of the fibrils as corresponding to such elements. By their union to form larger particles, as in the general process of colloid-coagulation, sufficient mechanical energy to account for contraction might conceivably be freed, since the reduction of surface-area in such a process may be very great, implying a correspondingly large transformation of surface-energy. It is known that in the precipitation of colloids by electrolytes a fundamental condition of the effect is a lessening of the contact-potential of the particles against the medium; the isoelectric point, where the contact-potential is zero, is typically the point of maximum instability, i. e., the tendency to fusion of the particles is then greatest; apparently their surface-energy, then no longer compensated by the electrical energy of the charged surfaces, draws the particles together until a new condition of equilibrium with lessened surface is reached. Increased surface-tension resulting from decrease or disappearance of the surface-charges is in fact now regarded as one of the chief conditions determining the union of the colloidal particles to form larger complexes. This union, if it proceeds sufficiently far, leads to the coagulation or precipitation of the colloid.

Now if in a contractile tissue the mechanical energy appearing in contraction is the expression of a temporary coalescence of the colloidal particles of the fibrils, due to their increased surface-tension, any condition furthering contraction ought, if not rapidly reversed, to lead to further fusion of particles and eventually to visible coagulation. Various facts of comparative physiology show that during conditions of extreme contraction the colloids of contractile tissues do frequently

undergo a more or less evident coagulation. The most striking instance known to me is that of the swimming plates of ctenophores; these structures, when immersed in pure isotonic solutions of sodium salts, exhibit for a short time an abnormally accelerated contractile rhythm accompanied by a progressive coagulation of the normally transparent contractile substance; this coagulation is the more rapid and complete the more energetic the contractile movements. Pütter in his recently published "Vergleichende Physiologie" cites (p. 456) a number of instances where contraction of muscle is accompanied by a visible coagulation of the muscle-substance. In vertebrate muscle the coalescence of colloidal particles—assuming it to take place—does not normally lead to visible coagulation during contraction. But it is characteristic of this tissue that the contraction is instantly and automatically reversed unless a rapid and rhythmical process of stimulation is continued. This peculiarity, which is perhaps the most remarkable property of this tissue, is favorable to, or at least quite consistent with, the view that a temporary coalescence of the colloidal particles occurs at each stimulation—due to a depolarization of the surface of the particles, simultaneously with a depolarization of the plasma-membrane of the entire cell—and that this coalescence is instantly reversed by the automatic return of the membrane to its normal polarized condition. If, however, the plasma membrane becomes *permanently* depolarized, as in consequence of any marked and permanent increase in ionic permeability (such as occurs during cytolysis), the coalescence of colloidal particles becomes permanent, and a visible coagulation, typically accompaned by a permanent shortening or "contracture," follows. Such an effect is produced if a frog's muscle is immersed in physiological salt solution containing saponin or other cytolytic substance. If the muscle is first sensitized by exposure for a few minutes to a pure isotonic solution of a sodium salt, such as iodide, the cytolytic action of the saponin is accelerated; the contraction is thus rendered quicker and

more energetic and the degree of coagulation is greater; *i. e.,* the energy of the contraction shows a distinct parallelism with the energy of the coagulative process in the muscle-substance. It might be maintained that the coagulative change is merely a secondary consequence of the cytolysis, and has no direct connection with the contraction, but when these facts are taken in conjunction with the others cited in this paragraph the indications seem strong that the ultimate process causing contraction is essentially the same as that which —if carried far enough—leads to coagulation of the colloids. As already pointed out, the latter process is due to fusion of colloidal particles to form larger aggregates; what causes the union appears to be heightened surface-tension resulting from diminished electrical surface-polarization; the increased tension then draws the particles together and thus performs a certain mechanical work. Similarly in the contractile tissue; within each fibril the colloidal particles or submicrons— which presumably are already in contact or cohere since the whole fibril forms a solid gel-like system—draw together more closely during contraction in consequence of a sudden increase in their surface-tension. This coalescence occurs only within each fibril, not between adjacent fibrils, hence the motion of displacement of the particles is virtually limited to the direction of the long axis and in consequence the whole fibril shortens. As the coalescence of the particles proceeds the active surface-area steadily decreases, and with it the contractile force; hence this force is greatest at the beginning of contraction and diminishes as the muscle shortens.

We assume therefore that in contraction the colloidal particles, especially those of the anisotropic segments, draw together or coalesce. There is, in other words, a clumping or flocking of the particles, which is most rapid and energetic in those regions where the particles are most numerous and closest together. In so doing they displace the more fluid interstitial substance. This incidental displacement of fluid is as necessary an accompaniment of the act of contraction as the coales-

cence of the particles, and if the contraction is to be rapid and quickly reversible the movement of the fluid must be equally so. It is this consideration, in my belief, which explains the advantage of the segmented structure. The fluid displaced from each anisotropic segment during coalescence of its particles gathers in the adjacent isotropic segments. These appear therefore to increase in volume during contraction (Hürthle), but the apparent transfer of fluid between these regions is merely the visible expression of its displacement from the anisotropic segments by the coalescing particles within the latter. Evidently the quickness and readiness with which the transfer of fluid occurs will increase with the area of the surface separating the two regions. The disposition of the contractile material of the fibril in numerous small denser segments separated by narrower segments of looser texture (i. e., with wider interstitial spaces) allows for the rapid displacement of the fluid by the colloidal particles as they coalesce; in other words, minimizes the resistance to such coalescence, and is hence a necessary condition for any rapid movement. In the reverse process of relaxation the original relative distribution of the solid and the fluid portions of the system is regained with equal readiness.

Conditions in a colloidal system of this segmented structure are thus highly favorable to rapid and promptly reversible contractile movements due to a massing or flocking of colloidal particles. The striated muscle-cell as a whole need lose no water in contraction; there is merely a temporary redistribution of the more fluid portion of the tissue within the cells. The case of the vertebrate smooth muscle fiber is different, and there is good evidence that in this tissue fluid does actually leave the cell during contraction. The characteristic slowness of both contraction and relaxation in smooth muscle may conceivably be explained on the supposition that the fluid displaced by the contraction of the intracellular fibrillar system can collect only in the relatively large intercellular spaces, i. e., must pass across the plasma membrane, instead of collecting in numerous minute intracellular spaces as in striated muscle. The transfer of fluid is thus necessarily gradual, and the contraction and relaxation are correspondingly slow.

The massing of the colloidal particles in the anisotropic segments results in a shortening and thickening of these segments and hence of the whole tissue. The advantage of having all the segments of the different fibrils within the same cell equal in size and situated at the same level becomes evident on further consideration. In a system of closely crowded contractile fibrils the mechanical processes in contiguous fibrils would clearly interfere with one another were this not the case. The overflow of the displaced fluid into the isotropic segments in any fibril would be impeded, and the coalescence of the colloidal particles thus checked or prevented, if during contraction the isotropic segments were in close contact with the anisotropic segments of other fibrils; as the latter thickened they would compress the isotropic segments of the fibril under consideration, and prevent the passage of fluid into these latter. Prevention of the displacement of fluid would however retard or prevent the coalescence of the particles, and hence the whole dependent contraction. Such interference between adjacent fibrils would obviously be minimal with a parallel disposition of fibrils, such as we actually find in the tissue. This arrangement is thus mechanically the most advantageous conceivable for a tissue whose effective action depends on the simultaneous contraction of a large number of closely crowded fibrils of the above conceived structure.

We conclude therefore that the physiological advantage of both the segmented structure and the parallel arrangement of the fibrils consists in the provision thus made for a rapid to-and-fro displacement of the fluid part of the fibrils during contractile activity. This displacement of fluid is, however, to be regarded as merely incidental to the contraction, and not as its immediate cause; and in this respect the theory supported above differs fundamentally from those according to which

the transfer of fluid is in itself the essential or " inogenetic " part of the process. It is of course obvious that any theory which (*e. g.*) regards contraction as due to a swelling of the isotropic segments by fluid absorbed from the anisotropic—as discs of gelatin or fibrin swell in acidulated water—must require that the interchange of fluid should be rapid and promptly reversible; hence that part of the present interpretation which regards the structure of striated muscle as essentially a means for facilitating transfer of fluid within the cell is equally consistent with this latter theory. Nevertheless the point of view that regards absorption of water by an acidulated sheet of gelatin as the analogue of what occurs in muscular contraction is radically different from that set forth in this paper, according to which the energy of contraction is the transformed surface-energy of the ultimate structural elements or colloidal particles (submicrons) composing the fibrils. There is undoubtedly a movement of fluid between the muscle-segments during contraction; but this fact in itself is consistent with either of the two theories just contrasted. The decision between the two must be made on the basis of other evidence.

<div align="right">RALPH S. LILLIE</div>

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FERTILIZATION OF THE EGGS OF VARIOUS INVERTEBRATES BY OX-SERUM

I

THE chemical method of artificial parthenogenesis has thus far been worked out with any degree of completeness, only for the Californian sea urchin, *Strongylocentrotus purpuratus.* In this form it was shown by Loeb that the process of fertilization is composed of two entirely different phases. The one is an alteration or destruction of the surface layer of the egg. This alteration of the cortical layer may or may not result in the formation of a fertilization membrane. The alteration of the surface can be brought about by a great many different means, all of which have a cytolytic effect. The superficial cytolysis starts the development of the egg but leaves the latter with a tendency to perish during the further development. The sickly condition is remedied by a second treatment of the egg, which may consist in putting the eggs for about from 30 to 50 minutes into hypertonic sea water of a certain concentration. If taken out of this solution, the egg develops practically normally.

Experiments on heterogeneous hybridization which Loeb carried out, furnished the evidence that the spermatozoon also causes the development of the egg by carrying two agencies into it, one of which is a cytolytic substance, a lysin, which causes the membrane formation.

Lysins are contained not only in the spermatozoon but in all the cells and in the blood of any animal. Loeb found five years ago that the blood of a worm, *Dendrostoma,* calls forth membrane formation in the unfertilizing egg of the sea-urchin. This blood retained its fertilizing power when diluted as much as several hundred times with sea water.

The same author found subsequently that the blood and tissue extract of many animals had the same effect, *e. g.,* the blood of cattle. The fact that the blood of each female does not cause the parthenogenetic development of its own eggs, Loeb explained by the theory, that while the lysins contained in the blood of foreign species can diffuse with comparative ease into the egg and the cells of an animal, the lysins contained in its own blood are prevented from such a diffusion.

It was found impossible to cause the development of the eggs of all female sea-urchins by means of foreign blood. This difficulty was overcome by treating the eggs with strontium chloride before they were exposed to the foreign serum. If the sea-urchin eggs were put for a short time into a $\frac{5}{8}$ or $\frac{5}{16}$ M solution of strontium chloride, a subsequent treatment with ox blood caused them all to form fertilization membranes. When subsequently treated for a short time with hypertonic sea water, most of the eggs developed into normal plutei.